Population growth & why we create models

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> "A model does nothing but expose the consequences of the assumptions upon which it is based."
>
> — Eric Schauber & Rick Ostfeld (2002) Ecol. Appl., 12(4):1142–1162

Exponential growth, the doubling model

We've seen the exponential model

$$N(t) = N_0 e^{rt}$$

Which describes the size of a population, N, starting from N_0 at time $t = 0$, and growing at an accelerating rate. Remember, if we take the logarithm of both sides we get

$$\log(N(t)) = \log(N_0) + rt,$$

Which is the equation for a line, like $y = mx + b$ with $y = \log(N(t))$, an intercept of $\log(N_0)$ and a slope of r (assuming we are using the natural logarithm). This formulation emphasizes the constant proportionality in growth of the population. A population grows from 10 to 100 in the same amount of time it takes to grow from 100 to 1000 or 1000 to 10,000.

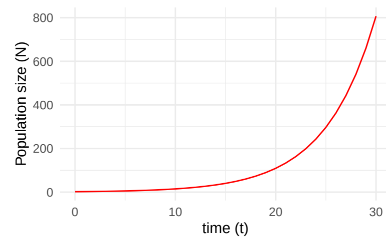


Figure 1: Population size over time, starting from $N_0 = 1$, in the exponential model with $r = 0.2$.

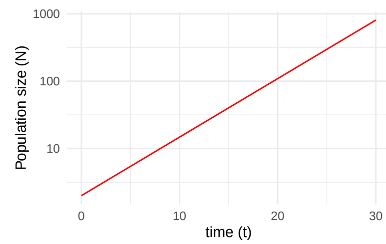


Figure 2: Same plot with a logarithmic y-axis.

The reason why becomes a bit clearer if we consider how the population *grows* (or shrinks) over time, rather than the actual size at any time. (In maths-speak, we're interested in the first derivative of the exponential model, $N(t) = N_0 e^{rt}$, we have been using so far. Or in reverse, the exponential model of $N(t)$ we have been using is the *solution* to the differential equation we're about to present. You do not need to remember your calculus, but rather just notice the relationship between the solution and the differential equation.) The differential equation for exponential growth is:

$$\frac{dN}{dt} = rN,$$

This equation translates into words as, "the rate of change in N, that is the *growth rate of the population*, is simply the *per capita* growth rate[1] times the population size." We'll come back to that *per capita* growth rate idea in a moment, but first, *Congratulations!* That was first model of population growth! Not so difficult, right?

[1] Or, if $r < 0$, the rate of decline.

Second, notice that larger populations grow faster, period. If the population size were $N = 1,000$ then the population would grow at rate $rN = r \times 1,000$. What if the population size was $N = 1,000,000,000,000$? No problem, the population grows at rate $rN = r \times 1,000,000,000,000$. Whatever N is, the population grows at rate rN.

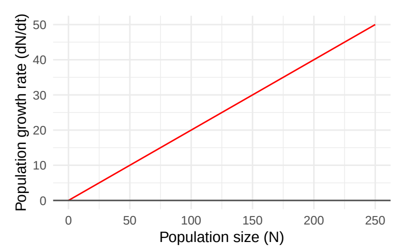


Figure 3: Population growth rate as a function of population size with $r = 0.2$ from the exponential model.

We can plot this relationship between growth rate and population size. As you would expect from what we just said in words, this relationship is just a straight line starting at zero[2] that goes up and up forever with a slope of r.

[2] With a population of zero, there is no one to reproduce!

A WORD OF WARNING: Be sure to pay attention to the axis labels. Before we were plotting N against time, but now we are plotting dN/dt against N. They show different things even though they might have similar lines.

Population growth rates vs. per capita growth rates

So this model and graph describes the growth of the population as a whole. What does this model say about the growth—as in *replication*[3] not *getting bigger*—of individuals? Well, if dN/dt is the population growth rate, then dividing it by N gives us the average growth per individual in the population (all N of them).

[3] Mean the average birth rate of from an individual minus the average death rate

$$\frac{dN}{dt} = rN$$
$$\frac{\frac{dN}{dt}}{N} = \frac{rN}{N} = r$$

So mathematically the average growth per individual in the population, also known as the *per capita*[4] growth rate, is just r. Always. Whatever else might be happening, no matter how big or small the population, individuals reproduce (and die) on average at rate r. A plot of per capita growth rate against N makes this clear; it always just r.

[4] From the Latin, by heads.

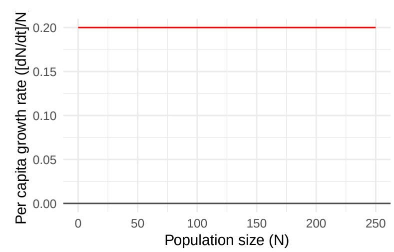


Figure 4: Per capita growth rate as a function of population size with $r = 0.2$ in the exponential model.

Problems in the land of exponential growth

The exponential model is very simple and quite useful, but does it not seem a bit, ummm, unrealistic? I mean, does it make sense that an individual in a real population of, say, elephants, would have the same number of offspring per year if she were surrounded by ten other females or ten thousand or ten million? Would there be enough resources for all of that reproduction? Enough room? Wouldn't the elephants run out of food and die?

Similarly, at the whole population level, does it make sense that the population just keeps growing faster and faster and faster over time, always doubling at the same rate no matter how big it gets[5]? In a word, no.

[5] You can extend the model well past the point where there are more elephants than atoms in the Galaxy, but that doesn't mean it makes biological sense.

The model is not wrong; it does what we told it to. We said, implicitly at least, that the per capita growth rate is just a constant, no matter what, which means that the population growth rate increases with population size. The model just revealed the consequences of the assumptions we built into it. But this assumption was quite unrealistic and so, eventually, are the dynamics of the model. Let's try again.

Before doing so, however, it is worth noting that every self-replicating thing—from computer viruses to real viruses to elephants—has the *potential* to grow exponentially. Look back to the essay on doubling to remember the consequences, how rapidly we might be neck deep in elephants if their population kept growing at a constant rate[6]. What keeps us from being knee deep in elephants or bacteria or, well, anything? That is what much of the field of ecology is about. But I bet you can come up with a few reasonable guesses.

[6] Well, rapidly relative to the tens of millions of years modern elephants arose.

The logistic model of population growth

Instead of assuming that per capita growth is a constant, let us acknowledge that at some point the individuals in the population are using all of the resources available.

Perhaps food or water or shelter or who knows what is limiting. Thus, when N gets big enough, there is just enough resources for individuals to replace themselves[7], meaning the per capita growth rate (and thus population growth rate) would be zero[8]. In a simplistic sense, there can be no (successful) reproduction unless someone dies to make room for that new individual. Let us call this population size where individuals *just* replace themselves k.

[7] On average. In reality, some might do really well and others poorly, but these effects balance out.

[8] Remember we are talking about growth rate, not λ, the population multiplier in a discrete time step model like you've seen elsewhere. When $\lambda = 1$, per capita growth is zero.

So we know the extremes—at low N per capita growth is r and a $N = k$ per capita growth is zero—but how do we connect these terms? We have many options. Three are shown in the figure to the right. At one extreme (line C) we could create a model where the per capita growth is unaffected by population size right up to the point where it goes to zero, like an on/off switch. This does not seem very reasonable, as just below k there is no effect of population size and then add one more individual and *bam!*, no more net growth! Instead, we might say that the effect of population size on per capita growth rate is negligible at low population sizes and then grows faster and faster (line B). That seems more reasonable.

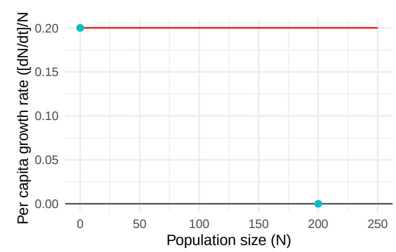


Figure 5: Per capita growth rate as a function of population size with $r = 0.2$ in the exponential model and a point at $N = 0$ where per capita growth is r, and one at $N = k = 200$ where per capita growth is zero.

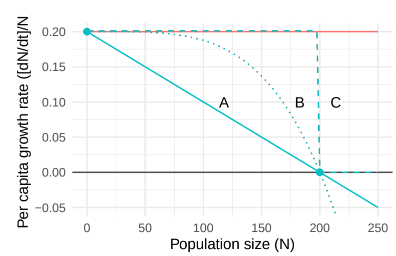


Figure 6: Per capita growth rate as a function of population size with $r = 0.2$ in the exponential model and three options for how we can reach zero per capita growth at $N = k = 200$.

The simplest option would be to say that per capita growth rates decline *linearly* with population size (line A). This is equivalent to saying that there is a finite pool of resources that gets divided more or less evenly among the N individuals, so with more individuals, each one gets fewer resources until they have enough to just replace themselves at $N = k$. This is the so-called "logistic" growth model and we can use it to revise our equation for per capita growth:

$$\frac{\frac{dN}{dt}}{N} = r\left(1 - \frac{N}{k}\right)$$

Let's walk through how this works, mathematically. First, if N is really small relative to k (either N is small or k is very big) then the stuff in parentheses becomes one minus something small, perhaps very small. If it is small enough then the stuff in parentheses is essentially one and we get our exponential model back. If we wanted to get fancy we could say that the exponential model is just a special case of the logistic model where $N << k$. But of course we wouldn't want to be fancy, would we? Second, we can see that when the population reaches k, then $N/k = 1$ so the stuff in parentheses becomes $1 - 1 = 0$. This has the effect of multiplying the intrinsic growth rate by zero, so the overall *per capita* growth rate is zero. Nice! Finally, note that if N gets bigger than k (and so $N/k > 1$) we end up subtracting a larger number from a smaller number, so the stuff in parentheses becomes *negative*. This means that if the population size is bigger than k the *per capita* growth rate goes negative! (If you are unsure of this, try plugging in some numbers for N and k, maybe $k = 200$ and $N = 1, 10, 100,$ and 200.) Neat! We added just one term, k, and we can get this nice behavior!

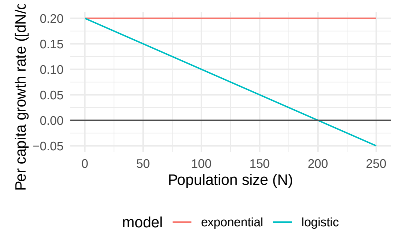


Figure 7: Per capita growth rate as a function of population size in the exponential model and logistic models with $r = 0.2$ and $k = 200$.

As an aside, this is one version of density-dependence, where a rate, here the *per capita* growth rate, is influenced by population size or density. That is, *something* about being around or part of a larger (or smaller) population changes something fundamental in the process. Here we are assuming that birth rates are reduced and/or death rates are increased with higher population densities, perhaps because the finite resources are divided up among more and more individuals. But there is nothing about the biological mechanism here. You might have heard of k being the "carrying capacity" of the environment, meaning something like the resources available in the environment, as is k somehow accounted for all of the food and shelter and so on in a place. But none of that is intrinsic to the model. All that extra meaning is applied to the the model by us, as biologists with some ideas of how things might work. The math just requires that *per capita* growth is zero when $N = k$. That's it.

Anyway, how does the *population* growth rate change with N? We can multiply both sides of the equation by N (the reverse of what we did above, with the exponential model) to get the differential equation describing population growth with density dependence.

$$\frac{\frac{dN}{dt}}{N} \times N = r\left(1 - \frac{N}{k}\right) \times N$$

$$\frac{dN}{dt} = rN\left(1 - \frac{N}{k}\right).$$

If we multiply the rN term on the right-hand side through the terms in the parentheses we get

$$\frac{dN}{dt} = rN - \frac{r}{k}N^2,$$

Which maybe pulls at your memory of math classes in the past. This is the equation for a parabola. And indeed, a plot of population growth rate against population size is parabolic.

You will see that the population growth rate is at first going up at about the same rate as the exponential model[9], but curves away from the exponential line more and more as N gets bigger. That is, the larger the population gets, the less it grows exponentially. That is the consequence of how we built this model. At $N = k$ the population growth rate is zero—that is, the population is stable—and beyond that it shrinks.

You will also see that the population growth rate is highest half-way to k. How do we explain this, when the highest per capita growth rate was when N was small? Well, the per capita growth rate is highest when population size is smallest,

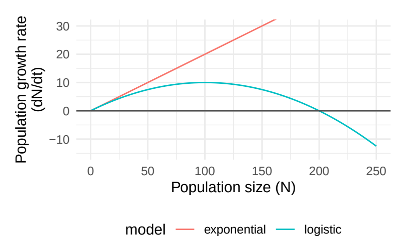


Figure 8: Population growth rate as a function of population size in the exponential model and logistic models with $r = 0.2$ and $k = 200$.

[9] And if we make k really, really big, then population growth in the logistic model will follow that of the exponential model over a much wider range. Think about what happens if $k = \infty$.

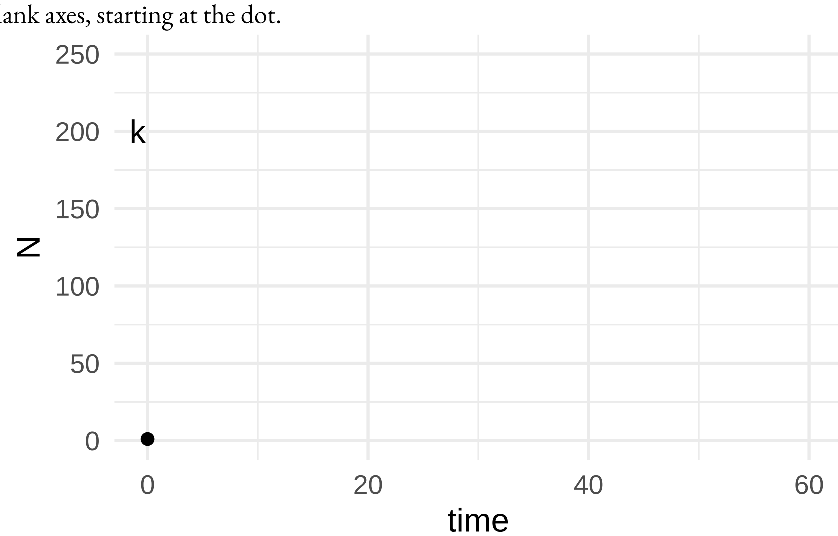
but then again, there are very few individuals replicating so quickly. At much higher population sizes there are lots of individuals doing the replicating, but each has a very small per capita growth rate. In the middle we get a moderate number of individuals replicating moderately, which happens to maximize the growth of the population as a whole.

Logistic growth dynamics

Finally, we might ask what the population size would be like over *time* given this model. Before showing it to you (though I expect many if not most of you have already seen the graph we'll make) it is worth thinking through what we would expect given our graph of population growth rates. Remember that the height of the line in this last graph of dN/dt is the slope of the line showing how N changes through time; low, but positive values of dN/dt mean flatter slopes (i.e., less change over time) and larger positive values of dN/dt mean a steeper slope. So…

- What would the curve of N over time look like if we started from a few individuals?
- What would the curve look like as N starts to get a bit bigger? As it gets to $N = k/2$?
- What would the curve look like as N gets closer and closer to k?

In fact, try sketching out your guess of population size through time on these blank axes, starting at the dot.



For completeness more than anything, here's the equation for solution to the logistic growth model[10]:

$$N(t) = \frac{k}{1 + \left(\frac{k}{N_0} - 1\right) e^{-rt}}.$$

You'll probably never need to use this, but if you like the math[11] you might see that as time, t, gets really big, the $-rt$ becomes a very large negative number, and so the e^{-rt} gets closer and closer to zero. So the stuff after the one in the denominator gets smaller and smaller, no matter what, when t is big. This means that $N(t \to \infty) \to k/1 = k$. We end up at k. Is that what you expected?

There we have it! The characteristic sigmoidal curve of population through time up to a "carrying capacity" we called k, is logistic growth. It's a curve you have almost certainly seen before, but now you see the underlying logic of it and how those assumptions we made lead to these dynamics. And it is your second model of population growth! A double woo-woo!

Do we see logistic growth in nature? You bet! For instance, in a classic set of experiments Russian biologist Georgii Frantsevich Gause studied the growth of several species of ciliates (bacteria-eating protozoans) and, in other experiments, yeast, grown in isolation and in combination. You can see how the logistic curves seem to capture the general dynamics of his ciliates. It's not perfect, but it's pretty darn good!

[10] This is called the logistic model because it "maps on to" (is a special case of) the logistic function. It describes many biological processes from dose effects to the prevalence of infection in a population when individuals do not recover. It's real workhorse!

[11] Yay math!

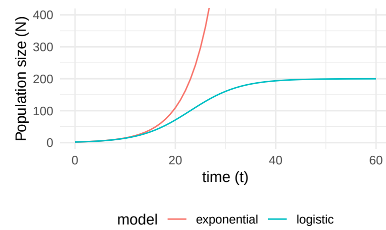


Figure 9: Population size over time, starting from $N_0 = 1$, in the exponential and logistic models with $r = 0.2$ and $k = 200$.

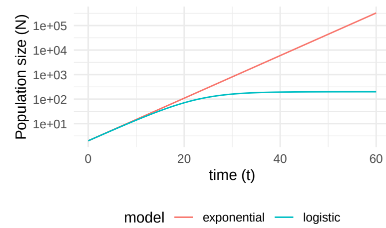


Figure 10: Same plot with a logarithmic y-axis.

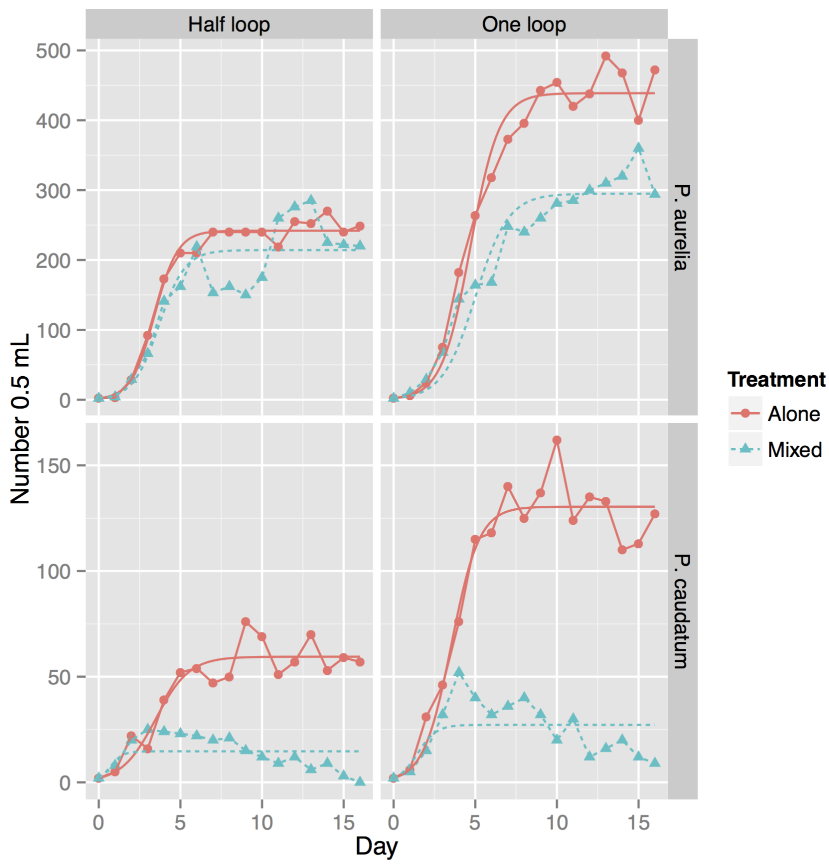


Figure 11: Gause's ciliates grown by themselves or in pairs with low food (half loop) or high food availability (one loop). Notice that when the food was doubled, the population size grew about twice as large.

Is the logistic model better?

In all my years of teaching about, sometimes jumping up and down excitedly about, population dynamics and these models, there is one question I *still* find hard to answer, but one I'm asked a lot. *If the logistic model is better than the exponential model, why do we even bother with exponential growth?* It's tricky because I get stuck on that one word, "better." What do we mean by better? More "accurate" or "realistic" or "useful"? In all of these cases we need to be clear about what we want and why. But really, at it's heart, this is a question that boils down to what are we using models for?

We actually construct models in science and more broadly for lots and lots of reasons Here's a partial, and somewhat overlapping list:

- To define the most important parts or processes in a system. This might just be a box and arrow sort of model or it might involve mathematics to represent those boxes and arrows. In any case, we want to set out how we think the system works.
- To clarify our assumptions about how a system works and express our ideas simply and clearly[12]. Words are so slippery, but when you pin down what you are thinking on a whiteboard or back of the envelope or whatever, you can see where you and someone else agree and where you part ways. Super useful!
- To understand the consequences of the assumptions you have embedded in a model. What happens if animals try to maximize their energy intake during foraging? How much of two alternative foods would they eat? What if they also had to avoid a predator?
- To see how complex behaviors emerge from simple interactions / try to see what is required to create patterns or behaviors of interest. The murmurations you might have seen in flocks of birds flying around together or schools of fish? Those can be described with three "rules" in an algorithm. The population cycles of lynx and hare, a classic example in ecology, can be described, more or less, with two fairly simple equations. Moreover, when a model *cannot* produce or reasonably describe the phenomenon of interest, that's interesting! If means you are missing something important.
- To compare systems. Rabies and influenza are of course very different viruses and so on, but perhaps their means of transmission are similar enough to suggest similar ways to intervene.
- To make predictions[13] about how a population or system will change in time or with interventions or so on. Or perhaps more accurately and usefully, *projecting* particular dynamics or mechanisms into the future, where the goal is less to generate accurate forecasts of, say, population size in the future and more to see how things might play out in the future under different scenarios.

[12] Another favorite quote: "There's no sense in being precise when you don't even know what you're talking about." - John von Neumann

[13] Most people tend to think about prediction when they're thinking of models. If a model does not do a good job of predicting the future, it must be crap, right? But scientists are usually focused on the other types of uses; models as tools of understanding.

So with some of these uses in mind, is the logistic model better than the exponential? I would argue that we have actually learned a lot from the exponential model. First, it *can* describe the early dynamics of some self-replicating process, at least in a stable environment *before* resources become limiting, predators or immune responses kick in, and so on. But perhaps more importantly, it shows us the potential for what *could* happen *if not for* limiting resources, predators, and so on. It is always, eventually, wrong, but it fails in an interesting and useful way. As such, it is a great starting place when thinking about a system or building a model (or teaching).

Now the logistic model adds one parameter[14], k, that provides us very different dynamics. It gives us a ceiling to growth, which is, in a sense, more realistic. This model also gives us a sense of how per capita and population growth change with population size, giving us greater intuition into how a system with density-dependent growth might work.

[14] The parameters, r and k, are sort of like tuning knobs. They control how quickly or slowly things happen or where stuff happens in the model, but not, overall, how the model works. There is only one (state) variable in the model, N, that changes or "evolves" (in the sense of unfolding) in response to model structure and parameter values.

But it is worth noting that this model is still a vast over simplification of reality. Sure it can describe the dynamics of population of certain systems, like bacteria in chemostats or virus in cell culture, but only so long as they are held under fairly constant conditions, there are no other organisms interacting (e.g., no bacteriophage or bacterivores or competitors, no immune response, etc.), and so on. If those other factors become important, this model, which does not include them, will probably miss the mark. But then again, it's pretty interesting to see how far we can get with this simple model before it fails to capture the dynamics of a system. And it becomes interesting to see what tweaks[15] it takes until some alternate version of this model does capture the essential dynamics, if that is even possible.

[15] A time delay? Stochastic variation in rates? Discrete time steps?

In the future we can discuss how models are used, why they are wrong, and why that can be a good thing. For now, I hope you see how we can alter a very simple model to create interesting new dynamics, how a model simply illustrates the results of the assumptions we build into it, and why even dumb models are useful. I also hope you feel like you can use these two models to make general statements about how populations might work. (It will be on the test![16])

[16] Well, not literally. But I would like you to be able to describe, use, and think with these two models for the DoM.